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BROMELIAD-EATING WEEVILS

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ABSTRACT. All known bromeliad-eating weevils—24 species in four genera (*Cactophagus, Cholus, Diastethus,* and *Metamasius*)—are native to the tropics and subtropics of the Americas. Several attack more than one bromeliad genus. Six are known to attack *Ananas comosus.* Four (*Metamasius dimidiatipennis, M. callizona, M. quadrilineatus,* and *M. sellatus*) have traveled far from their native ranges by hitchhiking in exported/imported bromeliads. *Metamasius mosieri* (a small weevil) attacks bromeliads of small stature, whereas *M. callizona* (a larger weevil) attacks bromeliads of larger stature. *Tillandsia utriculata* populations in Florida (USA) have suffered devastating attack by the immigrant weevil *M. callizona* (from Mexico), perhaps because these plants have evolved in isolation and have no method of resistance. A biological control campaign against *M. callizona* is in progress.

RESUMEN. Todos los picudos comedores de bromelias conocidas, los cuales pertenecen a 24 especies en cuatro géneros (*Metamasius, Cactophagus, Diastethus* y *Cholus*), son nativos de los trópicos y subtrópicos de las Américas. Varios atacan más de un género de bromelias. Seis atacan *Ananas comosus.* Cuatro (*Metamasius dimidiatipennis, M. callizona, M. quadrilineatus* y *M. sellatus*) han viajado lejos de sus ambientes nativos como "polizones" en bromelias exportadas e importadas. *Metamasius mosieri* (un picudo pequeño) ataca bromelias de tamaño pequeño, mientras *M. callizona* (un picudo más grande) ataca bromelias de mayor tamaño. Poblaciones de *Tillandsia utriculata* en la Florida (Estados Unidos) han sufrido ataques devastadores por el picudo inmigrante de México *M. callizona* quizas porque dichas poblaciones han evolucionado aisladamente y no tienen ningún mecanismo de resistencia. Una campaña de control biológico en contra de *M. callizona* está en progreso.

Key words: Bromeliaceae, Curculionidae, *Metamasius, Cholus, Cactophagus,* bromeliaphagy

INTRODUCTION

In a natural population of bromeliads, a large proportion of dead and dying plants is an uncommon sight, at least when insects are causing the damage. Although collectors of bromeliads may encounter numerous kinds of invertebrates living in leaf axils, few if any of these animals are detrimental to the plants. Even when lubber grasshoppers, *Romalea guttata* (Houttuyn), swarm in the Florida Everglades, the damage they do to the larger bromeliads seems to be largely cosmetic; leaves are severely chewed, but the plants are not killed.

Such observations, coupled thus far with the study of only a few insect species and those not known to damage bromeliads grown as ornamental plants, may have given rise to the popular misconception among growers that bromeliads lack consequential insect pests. Evidence in this paper suggests, to the contrary, that bromeliads in natural populations in the neotropics are attacked by phytophagous insects potentially lethal to the plants but that these insects generally have sparse populations. Among these insects are weevils (Curculionidae), which upon arrival in a previously unoccupied locality may cause severe losses to bromeliad populations, whether the plants are growing under natural or cultivated conditions.

The purposes of this paper—to review knowledge of the hostplant relationships of weevils that feed on bromeliads, to consider the ecology of these weevils under natural and altered conditions, and to document how some of them have become pests—may stimulate additional observations and research by canopy biologists.

WEEVILS THAT EAT BROMELIADS

Weevils (Curculionidae) are almost exclusively phytophagous. The more than 40,000 described species make them one of the largest families of beetles. The diversity of weevil species often is attributed to their special adaptations to diverse hostplants.

Adults and larvae of 24 species of weevils belonging to four genera (*Cactophagus, Cholus, Diastethus,* and *Metamasius*) currently are known or suspected to be specialized feeders on bromeliads (TABLE 1, with distribution records compiled from O'Brien & Wibmer 1982 and Wibmer & O'Brien 1986). Each of these 24 species is native to some restricted area of the tropics and subtropics of the Americas. Although two of the genera (*Cactophagus* and *Metamasius*) are closely related, the relationship of the other two genera is remote, indicating that "bromeliaphagy" evolved independently in several ancestral lineages of weevils.

TABLE 1. Weevils known to eat bromeliads, or that are suspected of doing so, with their distribution and hostplants in their native areas.

Weevil	Distribution	Hostplants
Cactophagus lojanus (Heller)	Bolivia, Brazil, Ecuador, Peru	?
Cactophagus miniatopunctatus Chevrolat	Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica	*Ananas comosus*
Cactophagus sanguinolentus (Olivier)	Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador	*Aechmea bracteata*
Cactophagus transatlanticus (Kirsch)	Costa Rica, Colombia, Ecuador, Venezuela	?
Cactophagus validirostris (Gyllenhal)	Mexico, Guatemala, Honduras, Panama, Colombia, Ecuador	*Aechmea bracteata, Vriesea* sp.
Cholus spinipes (Fabricius)	Grenada	*Ananas comosus*
Cholus vaurieae O'Brien	Venezuela	*Ananas comosus*
Diastethus bromeliarum Champion	Costa Rica	?
Metamasius alveolus Vaurie	Costa Rica	?
Metamasius bromeliadicola Champion	Costa Rica	?
Metamasius callizona (Chevrolat)	Mexico, Guatemala, probably not Panama despite old record	*Tillandsia deppeana, T. ehlersiana, T. heterophylla, T. limbata, T. roland-gosselinii, T. streptophylla, T. utriculata, Aechmea mexicana, Catopsis* sp. (see also text)
Metamasius ciliatus (Champion)	Mexico	*Aechmea bracteata*
Metamasius cincinnatus Champion	Nicaragua, Costa Rica, Panama, Ecuador	*Werauhia werckleana, Guzmania circinnata*
Metamasius dimidiatipennis (Jekel)	Mexico, Guatemala, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, French Guiana, Ecuador, Peru, Brazil	*Ananas comosus*
Metamasius fasciatus (Olivier)	Costa Rica, Panama, Venezuela, Ecuador	?
Metamasius flavopictus (Champion)	Mexico, Guatemala	*Tillandsia velickiana*
Metamasius hebetatus (Gyllenhal)	Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Ecuador, Peru, Bolivia	?
Metamasius mosieri Barber	Cuba, Dominican Republic, USA (Florida)	*Tillandsia balbisiana* (see also text)
Metamasius nudiventris Champion	Mexico, Nicaragua, Costa Rica, Panama	?
Metamasius quadrilineatus Champion	Mexico, Guatemala, El Salvador, Honduras	*Tillandsia guatemalensis, T. orogenes, T. ponderosa, T. standleyi, T. yunckeri, Racinaea spiculosa, Werauhia nephrolepis, W. pectinata, Catopsis hahnii, C. morreniana, Billbergia* sp.
Metamasius quadrisignatus (Gyllenhal)	Montserrat, Guadeloupe, Dominica, Martinique, Panama	?
Metamasius ritchiei Marshall	Cuba, Jamaica	*Ananas comosus*
Metamasius rugipectus (Champion)	Mexico, Costa Rica, Panama	?
Metamasius sellatus Champion	Mexico, Belize, Guatemala, Nicaragua, Panama	*Tillandsia guatemalensis*

TABLE 2. Weevils found attacking bromeliads in other-than-natural environmental conditions.

Weevil	Country	Plants attacked	Reference
Cactophagus miniatopunctatus	Mexico[1]	*Ananas comosus*	Vaurie 1967
Cholus spinipes	Grenada[1]	*Ananas comosus*	Marshall 1922
Cholus vauriae	Venezuela[1]	*Ananas comosus*	Salas & O'Brien 1997
Metamasius callizona	Mexico[2,3]	*Tillandsia* spp.	Frank & Thomas 1994b
	Mexico[1]	*Ananas comosus*	This paper
	USA (FL)[3,4]	13 genera	Frank & Thomas 1994b
	USA (FL)[5]	Native *Tillandsia*	Frank & Thomas 1994b
	USA (FL)[1]	*Ananas comosus*	Frank & Thomas 1994b
Metamasius cincinnatus	Panama[2]	*Werauhia werckleana*	This paper
Metamasius dimidiatipennis	Venezuela[1,6]	*Ananas comosus*	Salas et al. 1996
	Indonesia (Java)[4]	Imported bromeliads	Vaurie 1966
Metamasius mosieri	USA (FL)[3]	Imported *Tillandsia*	This paper
Metamasius ritchiei	Jamaica[1]	*Ananas comosus*	Marshall 1916

[1] Cultivated pineapples in beds or fields.
[2] Native bromeliads in habitats disturbed by humans (e.g., coffee plantations).
[3] Cultivated bromeliads in shade-houses or greenhouses or gardens.
[4] Imported bromeliads attacked by an adventive weevil species.
[5] Native bromeliads in native habitats (attacked by an adventive weevil species).
[6] Also in Costa Rica, Panama, and Ecuador (Vaurie 1966, Frank & Thomas 1994b.

Weevil larvae mine inside the stem, flowerstalk, or (in plants such as *Ananas*) the fruit. Although the presence of these larvae demonstrates bromeliaphagy by a weevil species, identification keys for weevils depend on characters provided by adults. Entomologists surveying the insect fauna of a region seldom bother to collect larvae, much less take time to rear them to the adult stage for identification. Adults feed externally on leaves, flowerstalks, and flowers. After developing through immature stages inside a plant, resultant adults disperse to detect other plants suitable for attack. During their dispersal, they may be found in other habitats and on plants that are not their hostplants, providing opportunity for misassociation of the hostplant. Entomologists who collect weevils are not necessarily adept at identifying plants, especially to the species level in tropical countries; nor will they necessarily collect plant samples for identification. The hostplants of many weevil species thus are unknown. Increased knowledge will come gradually aided by botanists who take the time to collect weevil larvae from identified bromeliads, rear the larvae, and present the resultant adult weevils to the few entomologists who specialize in weevil identification.

WEEVILS IN NATURAL AND ALTERED HABITATS

Metamasius

The available information on host-relationships of bromeliad-eating weevils is presented here, organized under the names of the weevils. Information on natural habitats and hosts precedes information on weevils in altered habitats, and the latter is summarized in TABLE 2.

Metamasius callizona

Vaurie (1966) examined one museum specimen of *M. callizona* labeled "Panama, Potrerillos, Dec., 1935." For the greater part of three weeks in June 1994, part of the time accompanied by A. Muzzell, the author searched unsuccessfully for that species in western Panama; nor were any specimens found in the insect collections housed in the Smithsonian Tropical Research Institute, Panama City. For lack of evidence and for lack of records from any other country south of Guatemala, the existence of *M. callizona* in Panama is doubtful (the specimen seen by Vaurie may have been mislabeled).

During more than two weeks of concentrated searching for *Metamasius callizona* in southern Mexico (mainly the state of Veracruz) in July 1992, M. Thomas and the author found a mere dozen specimens in fallen *Tillandsia streptophylla* Scheidw., *T. utriculata* L., and/or *T. limbata* Schltdl. The weevils were found in coffee plantations near Coatepec (19°26′N, 97°00′W), Veracruz (Frank & Thomas 1994a, 1994b). A search during several weekends from May to October 1995 in that same general area resulted in no greater success in numbers of specimens collected. Other Mexican records of *M. callizona* are from *Tillandsia roland-gosselinii* Mez in Oaxaca (Frank & Thomas 1994b), from *Aech-*

mea mexicana Baker in Veracruz and *Vriesia* sp. in Puebla (Zaragoza 1974), and from *Catopsis* sp. near Coatepec.

In 1992 and 1995, more than 60 *Metamasius callizona* weevils were found attacking bromeliads in a shadehouse of a grower in Veracruz, Mexico. Field-collected bromeliads had been assembled from various localities and concentrated in this shadehouse. The plants under attack included *Tillandsia deppeana* Steud., *T. ehlersiana* Rauh, *T. heterophylla* E. Morren, and *T. streptophylla.* Adult weevils have been intercepted several times, at least beginning in the early 1970s, in shipments of ornamental *Tillandsia* from Mexico at U.S. airports by U.S. Department of Agriculture, Animal and Plant Health Inspection Service (APHIS) inspectors (Frank & Thomas 1994b). Discovery of *M. callizona* in a nursery in Broward County, Florida, in 1989 (O'Brien et al. 1990) indicated that a contaminated shipment of ornamental bromeliads had escaped detection by APHIS inspectors. For the most part, the subsequent spread of *M. callizona* to 12 counties in southern Florida has been documented (Frank & Thomas 1991a, 1991b, 1994b, Frank 1997). The Florida native bromeliads on which *M. callizona* has been seen to feed include *T. fasciculata* Sw., *T. paucifolia* Baker, and *T. utriculata.* All three species have been placed (or are in process of being placed) on the Florida list of endangered species (Florida Administrative Code) because of attack by this weevil. The most severe losses thus far have been to *T. utriculata* whose populations in several areas have been devastated (Frank 1997).

In southern Florida, *Metamasius callizona* is now feral and has attacked cultivated bromeliads growing outdoors and in greenhouses. The plants attacked include representatives of *Aechmea, Ananas, Canistrum, Cryptanthus, Dyckia, Guzmania, Hohenbergia, Neoregelia, Nidularium, Orthophytum, Quesnelia, Tillandsia,* and *Vriesia* (Frank & Thomas 1994b). The weevil therefore may be capable of attacking the rarest of Florida's native bromeliads, once it reaches their highly restricted ranges in the Everglades region of southwestern Florida. These bromeliads are *Catopsis berteroniana* (Schult. f.) Mez, *C. floribunda* L.B. Sm., *C. nutans* (Sw.) Griseb., *G. monostachia* (L.) Rusby ex Mez, *T. flexuosa* Sw., and *T. pruinosa* Sw. Because the cultivated plants attacked include pineapple, it may be asked whether this weevil attacks pineapple in Mexico. An unconfirmed report suggests that it does so, but the attacks are restricted to pineapples growing near field edges in recently deforested areas.

Metamasius cincinnatus

At Fortuna (8°43′N, 82°16′W) and Boquete (8°47′N, 82°26′W) in the western province of Chiriquí, Panama, *M. cincinnatus* was encountered by the author in June 1994. During one week at Fortuna, a few specimens were found in mines in stems of *Guzmania circinnata* Rauh and of an unidentified *Vriesia* (not in flower). During three days at Boquete, nearly 100 specimens were found in mines in *Werauhia werckleana* (Mez) J.R. Grant still attached to fallen limbs of trees. The rarity of *M. cincinnatus* is attested not only by my failure to obtain more than 100 specimens during examination of hundreds of bromeliads at many localities in western Panama during a 3-week search, but also because it was unrepresented in the collections of the Smithsonian Tropical Research Institute.

Metamasius dimidiatipennis

There are no published records of this species from bromeliads in natural habitats. In Costa Rica, Panama, Ecuador, and Venezuela, it has been reported to attack pineapple (Vaurie 1966, Frank & Thomas 1994b, Salas et al. 1996). Specimens examined by Vaurie (1966) included two collected in 1923 from Indonesia. *Metamasius dimidiatipennis* may well have arrived in Indonesia as a contaminant of planting stock of ornamental bromeliads or pineapples.

Metamasius mosieri

A few specimens of *M. mosieri* infesting *Tillandsia balbisiana* Schult. f. were encountered by the author in southwestern Florida. The larvae seem to have the habit of mining the flowerstalks of mature plants. Only four adult specimens are present in the Florida State Collection of Arthropods, and these lack hostplant data (Frank & Thomas 1994b).

Specimens of *Metamasius mosieri* seldom have been collected in nature, and these only in *Tillandsia balbisiana*; but a bromeliad grower in Lee County, Florida—with a collection of imported bromeliads mainly in shadehouses but with a few attached to trees—has had some plants attacked by *M. mosieri.* Imported bromeliads attacked in that collection include *T. bergeri* Mez, *T. bulbosa* Hook., *T. concolor* L.B. Sm., *T. geminiflora* Brongn., *T. gardneri* Lindl., *T. hondurensis* Rauh, *T. ionantha* Planch., *T. jucunda* Castellanos, *T. rhomboidae* André, *T. streptophylla, T. stricta* Sol. ex Ker Gawl., and *T. vernicosa* Baker. All of these species, like *T. balbisiana,* are of small stature. None of these bromeliads could hold water in axils except on rainy days or shortly thereafter, because the axils have but trivial volumetric capacity, a few

drops; and none of them is a true tank bromeliad, even when fully grown.

Metamasius mosieri originally was described from Florida and Cuba (Barber 1920) and subsequently was found in the Dominican Republic. Its arrival date in Florida from Cuba or the Dominican Republic is unclear. If hundreds or even thousands of years ago, as is possible, then *M. mosieri* may be considered a species native to Florida. If, however, the weevil arrived within the last 400 years, then it would be considered adventive. Its small populations, despite having been present since before 1920, and its restriction to southwestern Florida suggest that its natural diet may be limited to *Tillandsia balbisiana,* which likewise has small populations and a restricted distribution. The weevil may or may not have specialist natural enemies in Florida. With so few specimens collected, the limits of detection of natural enemies may not have been reached.

Metamasius quadrilineatus

Between January 1995 and July 1996, R. Cave harvested 424 larvae and 60 pupae of *M. quadrilineatus* from 6920 fallen bromeliads in Honduran cloud forests. The sampled plants included *Tillandsia guatemalensis* L.B. Sm., *T. orogenes* Standl. & Williams, *T. ponderosa* L.B. Sm., *T. standleyi* L.B. Sm., *T. yunckeri* L.B. Sm., *Racinaea spiculosa* (Griseb.) M.A. Spencer & L.B. Sm., *Werauhia nephrolepis* (L.B. Sm. & Pittendr.) J.R. Grant, *Catopsis hahnii* Baker, and *C. morreniana* Mez (Cave 1997). Additional hostplant records for this weevil are from Chiapas, Mexico: *T. guatemalensis* (Lucas 1975), *Billbergia* sp., *Tillandsia* sp., and *W. pectinata* (L.B. Sm.) J.R. Grant (=*Vriesia chiapensis* Matuda) (Zaragoza 1971). Adults have been intercepted in shipments of ornamental *Tillandsia* from Mexico or Central America at U.S. airports by APHIS inspectors (Frank & Thomas 1994b).

Metamasius ritchiei

Neither adults nor larvae of this species have been reported from bromeliads under natural conditions. Its life cycle was investigated in Jamaica where the weevil was found to attack pineapple plants growing under shaded conditions, as when overgrown by weeds (Marshall 1916, Gowdey 1923, Reid 1960). Discovery of this damage to pineapples aroused concern in Florida, where pineapple production was an important industry, and the perceived threat of the arrival of *M. ritchiei* in Florida stimulated creation of the Florida State Plant Board, later called the Division of Plant Industry (Newell 1917). Ironically, this species did not arrive in Florida when pineapple cultivation was a major agricultural activity; *M. callizona* arrived instead. Only much later, when the growing of ornamental bromeliads had become an important horticultural activity (and pineapple production had almost disappeared) did *M. ritchiei* arrive; and now *M. callizona* attacks pineapple in Florida.

Metamasius sellatus

This species of weevil has been collected from *Tillandsia guatemalensis* in Chiapas, Mexico (Lucas 1975). *Metamasius sellatus* is one of the species that, like *M. callizona* and *M. quadrilineatus,* has been intercepted in shipments of ornamental *Tillandsia* from Mexico or Central America at U.S. airports by APHIS inspectors (Frank & Thomas 1994b). In 1995, the author collected several *M. sellatus* specimens from flowers of *Heliconia bourgaeana* Petersen in Veracruz, Mexico. The weevils were not observed feeding on the flowers, although they could have been taking pollen or nectar. *Heliconia* thus should not be thought of as a hostplant for this weevil.

Other *Metamasius* species

Metamasius ciliatus has been reported from *Aechmea bracteata* (Sw.) Griseb. in Veracruz, Mexico (Zaragoza 1974); *M. flavopictus* has been collected from *Tillandsia velickiana* L.B. Sm. in Guatemala (specimen and hostplant information supplied by D.J. Cathcart). Hostplants for the remaining bromeliad-eating species appear to be unreported under natural conditions. Many *Metamasius* species feed on plants other than bromeliads (Vaurie 1966).

Other Weevils

Cactophagus

Host records are *C. validirostris* from *Aechmea bracteata* in Veracruz, Mexico, and from *Vriesia* sp. in Puebla, Mexico, and *C. sanguinolentus* from *A. bracteata* in Veracruz (Zaragoza 1974). Other species of the genus have been reported from bromeliads, but the bromeliads were not identified specifically; other *Cactophagus* species feed on plants other than bromeliads. The name *Cactophagus* was coined because a few of the species attack cactus. *Cactophagus miniatopunctatus* has been reared from pineapple in Veracruz, Mexico (Vaurie 1967).

Diastethus

The name *D. bromeliarum* suggests the collection of specimens from a bromeliad and per-

haps bromeliaphagy, but no information was found about this species nor any of the five other *Diastethus* species known from Mexico and Central America.

Cholus

There is a dearth of information about natural hostplants of bromeliad-eating *Cholus* species. *Cholus spinipes* was reported (under the synonym *C. wattsi* Marshall) as a pest of pineapple growing in poorly tended, shaded conditions in Grenada, West Indies (Marshall 1922). Eggs are laid in the flowerstalk, which the larvae mine; they sometimes mine the fruit. Adults feed on fruits, stalks, and leaves. A second species, *C. vaurieae,* has similar habits in Venezuela (O'Brien 1994, Salas & O'Brien 1997). Host plants other than pineapple have not been reported for these two species; their presence was noted only when they attacked pineapple growing in monoculture in an altered environment. Other species of *Cholus* attack palms, grasses, and orchids; but none has been reported to attack bromeliads (Vaurie 1976).

Discussion

Since native plants and insects of any natural area are the result of an evolutionary process that may have taken thousands of years to reach its present state, any plant that could not coexist with insect fauna no longer exists in that area. The current population densities of the plants and their insect herbivores are interdependent. If a specialist insect herbivore limits the population of a plant species, then the plant population would be expected to expand if the insect were removed. It is not surprising then that bromeliads growing in the wild in the neotropics are not seen to be heavily attacked and killed by some native insect. Typically each herbivorous insect species has assorted natural enemies (predators, parasitoids, parasites, and pathogens) that attack it and limit its population.

When natural ecosystems are disrupted by human activity, populations of some species may expand, while others may decline. Humans may introduce non-native species, causing further change. Other (immigrant) species arriving by natural means may be able to establish populations, sometimes as a consequence of changes caused by humans. Yet other immigrant species are able to hitchhike in cargoes imported by humans or in the vehicles used to transport the cargoes (Simberloff et al. 1997, including Frank et al. 1997). Establishment of an herbivorous insect species, especially when it comes without the natural enemies that hold its population in check in its homeland, may threaten the plants on which it is able to feed in its new range (the place to which it has immigrated). Evidence (Frank & McCoy 1992) indicates that pest insects immigrating to Florida seldom arrive with the specialist natural enemies of their homelands. The founding members of an overseas plant population most likely have survived an arduous journey; they are few in number and healthy (free of parasitoids, parasites, and pathogens).

Natural Populations

Natural populations of epiphytic bromeliads and weevils have been found in Honduras, Mexico, and Panama. Those in Honduras were in remnants of cloud forests scattered about land that had been cleared for agriculture. Those in Mexico were in extensive coffee plantations, where many of the larger trees were left to provide shade, but all undergrowth was cleared and planted in coffee. Fallen bromeliads were cleared routinely from the ground, together with weeds. Those at Boquete, Panama, (a weevil-producing site) were on sparse roadside trees in an area cleared for agriculture. Only those at Fortuna, Panama, (a site with few weevils) were in an extensive forest preserve with no recent disturbance. These few observations do not give an adequate picture of the density of weevil populations relative to numbers of bromeliads sampled.

We can conclude that weevil population density varied from place to place, but nowhere was it as dense as that observed during invasion of *Metamasius callizona* in previously unoccupied areas of Florida. We can perhaps conclude that the densest populations were in some way isolated from continuous forest as at Boquete, Panama; in cloud forest remnants in Honduras; and in the shadehouse of a grower in Mexico. We can perhaps conclude that the traveler in those countries is unlikely to find dense weevil populations in areas with extensive forest (either natural or with undergrowth cleared for coffee trees), despite dense bromeliad populations.

Weevil Attacks and International Hitchhiking

Six species (*Cactophagus miniatopunctatus, Metamasius callizona, M. dimidiatipennis, M. ritchiei, Cholus spinipes,* and *C. vaurieae*) have been reported to include pineapple in their hostplant range. With some of the weevils, the threat to pineapple is greatest in shaded areas around field edges and where pineapples have become shaded by weeds. Two instances (the arrival of *M. dimidiatipennis* in Indonesia and of *M. calli-*

zona in Florida) threaten pineapples grown far from the native range of pineapple. Other instances raise questions of how long pineapple has been cultivated in Costa Rica, Panama, Colombia, Venezuela, Ecuador, and more so in Grenada, Jamaica, and Mexico. Another question concerns whether any of these weevils accomplished their distribution with the help of human intervention.

Risk faces pineapple industries elsewhere. For example, Hawaii, among all the states of the USA, has the worst record of invasion by adventive species of animals and plants, proportionately exceeding that of Florida (U.S. Congress 1993). Hawaii has an active trade in ornamental bromeliads that could provide a means of hitchhiking by weevils. For example, a bromeliad-inhabiting mosquito native to Florida (*Wyeomyia mitchellii* [Theobald]) became established in Hawaii before 1980 (Shroyer 1981).

Native bromeliads assembled in shadehouses may be attacked by native weevils (*Metamasius callizona* in Veracruz, Mexico). Imported, ornamental bromeliads in such locations may be attacked by native (*M. mosieri* in southwestern Florida) or adventive, feral weevils (*M. callizona* in southern Florida and perhaps *M. dimidiatipennis* in Java, Indonesia). Many other instances likely have gone unreported. The circumstances include the packing of many bromeliads into a small area and, perhaps, the exclusion of natural enemies that might in nature limit populations of the weevils.

Metamasius dimidiatipennis and *M. callizona* have established populations in areas far from their homelands, in Java (Indonesia) and Florida (USA) respectively. Interceptions by APHIS inspectors of ornamental bromeliads from Mexico and Central America have shown shipments to be infested by *M. callizona, M. quadrilineatus,* and *M. sellatus.*

Hostplant Range

At present, the weevil species listed in TABLE 1 are not believed to feed on any plant other than bromeliads. Females of some, such as *Cactophagus validirostris, Metamasius callizona, M. cincinnatus,* and *M. quadrilineatus,* evidently will oviposit on (and their larvae develop in) bromeliads of several genera in their natural habitats. Some, such as *M. callizona,* have been shown to attack an even wider range of bromeliad genera under unnatural conditions. It may not be assumed, however, that all of these weevils will feed on bromeliads of all genera, or even all bromeliads of one genus. Bromeliads of small stature—all *Tillandsia recurvata* (L.) L., *T. setacea* Sw., *T. usneoides* (L.) L., or young plants of *T. utriculata*—simply do not provide adequate tissue for development of the larvae of *M. callizona,* whose adults are moderately large. These plants seem not to be oviposited in by the female weevils; the most heavily attacked in nature in Florida are large plants of *T. utriculata.* Further, far fewer weevils of this species have been found in *T. fasciculata* than in *T. utriculata* in the field in Florida, no matter that *T. fasciculata* is in some places more abundant and grows almost as large, suggesting a preference for *T. utriculata.*

Conversely, female *Metamasius mosieri* seem to oviposit in *Tillandsia balbisiana* in nature in Florida, avoiding the much larger food source provided by large *T. fasciculata* and *T. utriculata* but accepting imported *Tillandsia* of small to moderate stature as alternative oviposition sites. Adults of *M. mosieri* are considerably smaller than those of *M. callizona,* so evidently their larvae need much less plant material in which to mine and develop than do larvae of *M. callizona.* Larvae of *Cholus vaurieae* are much larger than those of *M. callizona* and presumably would need a still greater bulk of plant material in which to mine and develop; thus far they have only been found in pineapple stems and fruits. Much remains to be learned about food needs and preferences.

Do Weevils Kill Plants?

In Florida, mining of *Tillandsia utriculata* stems by *Metamasius callizona* larvae causes the stems to break during wind and rain and the plants to fall to the ground, dying. Similarly, bromeliad growers in Florida report that at least some ornamental bromeliads are killed outright by larvae of *M. callizona.* In contrast, *M. mosieri* seems to mine the flowerstalks of *T. balbisiana,* leaving the plants alive and able to produce a new flowerstalk. Although *M. callizona* larvae can destroy parent plants of *T. fasciculata* and some ornamental bromeliads in Florida, the plants may be stimulated to produce viable offsets. In Florida, *T. utriculata* seems to rely upon seed for reproduction and rarely produces offsets. Thus the devastation caused by *M. callizona* in Florida may be the result of the weevil's attack on susceptible bromeliad populations that have not evolved to resist attack by such an insect. One method of defense by *T. utriculata* would be to produce offsets, and it is noteworthy that it does not do so in Florida but does so in Guatemala where bromeliad-eating weevils exist naturally (Isley 1987).

Metamasius callizona has had a devastating effect on natural populations of *Tillandsia utriculata* in Florida by destroying the larger plants,

i.e., the breeding population (Frank & Thomas 1994b). This effect can only worsen as the weevil population spreads. Further, as the weevil population encroaches on the Everglades, it will encounter Florida's rarest bromeliad species, some or all of which likely will be susceptible to destruction by it. Without the introduction and establishment of a successful biological control agent to limit the weevil population, Florida populations of some of these bromeliad species may be driven to extinction. In contrast, populations of bromeliads of small stature such as *T. recurvata, T. setacea,* and *T. usneoides* likely will suffer only from trivial cosmetic damage caused by occasional nibbling by adult weevils. Feeding by the adult insects alone can destroy such plants when weevils are confined with them alone and no other food, but weevil populations in nature likely will not be dense enough to do this.

Bromeliad societies at all levels have contributed funds and mounted Internet and print campaigns to alert growers to the damage caused by *Metamasius callizona* and other bromeliad-eating weevil pests in Florida. Such publicity is spreading the word on the risks of imported bromeliads contaminated by weevils and other pest insects. The best safeguard may be to dip all bromeliads to be exported in a suitable pesticidal solution and to repeat the dipping at the place of arrival. The best test of the publicity's effectiveness may be inspection of APHIS records to discover whether weevils intercepted in shipments of bromeliads have declined. If no marked decline in interceptions occurs, the next step would be to deny export/import permits to people who will not comply with the recommended dipping.

Food Pyramids and Biological Control

If knowledge of weevils that eat bromeliads is poorer than knowledge of bromeliads, then knowledge of organisms that kill the weevils is even poorer. The fungal entomopathogen *Beauveria bassiana* (Balsamo), which attacks many insects, was found on some *Metamasius callizona* from Mexico. Ants have been seen eating accidentally exposed weevil larvae, and perhaps some of the predatory organisms found in bromeliad leaf axils in the neotropics (such as frogs, lizards, scorpions, and earwigs) eat weevil adults or larvae (Frank & Thomas 1994b). The only specialist organism known to attack weevils that eat bromeliads is a yet-undescribed parasitoid fly of the genus *Admontia,* discovered in Honduras (Cave 1997). Its only known host at present is the larva of *M. quadrilineatus.* Perhaps this species also will attack *M. callizona.*

The localities mentioned in Honduras, Mexico, and Panama were rich in bromeliads. The collection of thousands would have been easy at many of them, but only at a few sites were weevils detected, and only at sites in Honduras were specialist parasitoids detected. There is no obvious way to locate sites with abundant parasitoids. They may be present at many forested sites with low-density populations of weevils, but if the weevils are uncommon then the parasitoids will be still less common because they are higher in the food pyramid. At some of the few, isolated sites with relatively abundant weevils, these insects may have been abundant precisely because of the absence of parasitoids. Detection of weevil-eating *Admontia* at Honduran sites, therefore, was a fortunate event which otherwise could have required greatly increased effort and cost in searching. Funds permitting, research is planned on rearing methods for *Admontia* and, if it will attack *M. callizona* but no non-target organisms, on introducing it into Florida and measuring its effects (Frank 1997).

Collaboration by Canopy Biologists

Bromeliads are attacked in nature by weevils and by other pest insects. Among them are larvae of Lepidoptera (butterflies and moths) which could possibly cause highly consequential damage. No review of such insects has yet been written. The same recommendations—dipping of exported/imported plants in chemical pesticides—should reduce or eliminate risk from them.

This paper exposes tremendous gaps in knowledge of weevils and other insects that eat bromeliads. Those who are in the best position to fill many of the gaps are canopy biologists who work with epiphytic plants and their associated insect faunas. Entomologists who take little interest in plants and botanists who take little interest in insects are in an inferior position, especially if they do not have ready access to epiphytic bromeliads growing in tree canopies.

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